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Steps to operationalize a rewilding decision: Focus on functional types

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If transparent and inclusive stakeholder discussion delivers a consensus for active rewilding, then five steps are recommended for operationalizing that decision, focused initially on the large herbivore assemblage. Consideration of large predators could follow, contingent upon the establishment of prey populations. First, determine the potential biomass density (kg/km^2) of large mammalian herbivores in the target landscape. Regression models based on rainfall or primary productivity are helpful if applicable, otherwise comparative studies are needed. Second, use empirical data from reference ecosystems to apportion biomass density among functional types, crudely defined by body size and feeding type (grazer, browser, mixed feeder). Third, identify specific functional traits (coarse grazing, endozoochory, etc.) of particular local importance. Fourth, identify species within each functional type that are already present, estimate their potential biomass densities, and thus identify the shortfall within each cell of the body size x feeding type matrix. A candidate set of native and non-native (surrogate) species is then identified to make up the shortfalls. This is followed by an iterative process of estimating equilibrium population sizes, stakeholder acceptance, and viability of each potential population. Fifth, stakeholders must be inclusively re-engaged to visualize the potential assemblage, its expected functional interactions, the ecosystem services to be delivered, and the long-term costs (including opportunity costs) and benefits. When a plan is supported, local stakeholders should be integrated as active participants in the implementation, monitoring, and championing of *their* rewilding project.

KEYWORDS

large herbivores, surrogate species, herbivore biomass, herbivory traits, ecosystem function, stakeholder engagement

1. Introduction

One of the greatest challenges facing humanity in the Anthropocene is the diminishment of ecosystem services. Addressing the challenge involves two thrusts: first, the alleviation of anthropogenic forcing on natural systems; second, the repair of ecosystem function. The first is replete with wicked problems for the global populace and so my focus here is on the second, which for decades has been the domain of restoration ecology. However, it is increasingly apparent that, despite the best efforts of restoration practitioners, their successes are hard-won and then chronically vulnerable to back-sliding. This is because any benchmark state that existed prior to a transformational disturbance is subsequently elusive due to a set of quaintly-named effects in ecosystem dynamics. One is the Humpty-Dumpty effect, meaning that after a complex system has fragmented, it cannot be reassembled in the way it once was because the *parts* (predators, prey, habitats, etc.) have undergone quantitative and qualitative change (Pimm, 1991; Evans et al., 2022). Another is the hysteresis effect, which arises because *feedbacks* among processes within the system have changed, causing the "return" trajectory to be different from the "departure" (Beisner et al., 2003). Then, the Red Queen effect (Van Valen, 1973) can apply at the ecosystem level, meaning that because the *environment* is always changing the system must continually reorganize and adapt if it is to persist within state thresholds.

I suggest it is pragmatic to find ways of working with, rather than against, the above effects especially where stakeholder-desired outcomes are dependent on ecosystem function. Identify what ecosystem services are required from an ecosystem, which ecosystem processes generate them, and which functional types of organism maintain those processes, before choosing which species to invest conservation resources in. This is where the rewilding concept (Pettorelli et al., 2019) is making advances, with (depending on one's definition of choice) its focus on functional type composition and acceptance of continual change and reorganization. To operationalize the concept for an ecologically degraded landscape, it is first vital to initiate a facilitated process of fully-inclusive stakeholder engagement. This is to reach consensus on which of three options is best aligned with the stakeholders' priorities: (1) restoring historical species composition; (2) enabling some future state of undefined wildness to evolve; or (3) repairing ecosystem function. A decision tree can be used to move forward with each of those options (du Toit and Pettorelli, 2019) but here I focus on the case of ecosystem function being the priority for an area where the stakeholder consensus is for active rewilding (Option 3). Also, it is assumed that the project area is degraded to the extent that the large mammal community is diminished, with large predators being absent or rare. Then, recognizing the impossibility of identifying all the elements and interactions involved in an ecosystem's function, a start can be made with the functional types represented by large herbivores (>5 kg body mass). A natural assemblage of syntopic large herbivores typically includes a relatively modest number of species (seldom >10) that can interactively impose strong top-down modifying effects on vegetation structure and composition, and on biogeochemical cycling (Vynne et al., 2022). Large herbivores are also visible and relatable agents of natural processes, thus facilitating a bond between stakeholders and *their* rewilding project. Developing an appropriate assemblage should happen within an adaptive co-management framework and with a social license to operate, so that practitioners and stakeholders may establish a trusting relationship (Butler et al., 2021). Concurrently, the technical team needs to follow a logical process to estimate how many of which large herbivore species would be required for the rewilding project, as suggested–with due recognition of knowledge gaps–in the steps that follow.

2. Steps for assembling a functionally diverse community of large herbivores

2.1. Estimate total potential biomass density

Macroecological meta-analyses have confirmed that in the absence of major anthropogenic distortions, the biomass density of an intact large herbivore community is generally expected to vary as a function of primary productivity, which in turn varies as a function of mean annual rainfall. That expectation currently holds in Africa, whereas on other continents the biomass of indigenous large herbivores is anthropogenically depleted (Fløjgaard et al., 2022). Fortunately, aerial survey data from African wildlife areas date back to the colonial era and enable a predictive understanding of the consumer-producer relationship. Coe et al. (1976) found a linear relationship by which variation in the logarithm of mean annual rainfall explained 77% of variation in the logarithm of large herbivore biomass density across wildlife and pastoral systems in the savannas of eastern and southern Africa. That relationship is, however, strongly influenced by soil nutrient status and 82%–85% of the variation can be explained by separate models for "low" and "medium to high" soil nutrient classes (Fritz and Duncan, 1994). Then, the diluting effect of rainfall means decreasing forage quality in wetter savannas, depressing herbivore biomass density from its peak of ~1,700 kg/km^2 (for wildlife excluding elephants, *Loxodonta africana*) in areas receiving >700 mm of mean annual rainfall (Hempson et al., 2015). Also, on a global scale, potential stocking rates can be estimated from remotely sensed data on net primary production in grasslands (Piipponen et al., 2021), although that underestimates community biomass because browsing is not accounted for.

Overall, evidence confirms that large herbivore biomass is controlled from the bottom up by food availability and mechanistic models can explain the relationship to the extent permitted by available data. Where the predator guild is intact, populations of smaller ungulates (<150 kg) are regulated by predation (Sinclair et al., 2003) but this would not (yet) occur where rewilding projects are being planned. Across ecosystems that are anthropogenically distorted, there is a need for standardized open-access data-bases of equilibrium densities of large mammals in reference areas such as national parks. Such data would not necessarily provide a local benchmark for target conditions in a geographically similar area, but could be used to guide rewilding projects in any area where the state of the ecosystem is forecast to be similar to the current state in the reference area over a timeframe that is meaningful to stakeholders. Meanwhile, rewilding should progress through an adaptive management cycle (Figure 1) for which an estimate of potential biomass density is only initially useful as an upper "ball-park" value to begin planning within.

2.2. Allocate biomass to functional types

Having an idea of potential biomass density, even if a ball-park estimate, allows the functional composition of a (yet notional) large herbivore community to be sketched out. As stressed by Bell (1982) in his seminal work on community structure in African savannas, mean annual rainfall and soil nutrient availability interact in ways that govern both the total biomass of large herbivores and the structure of the community (see also East, 1984). Areas of relatively low-quality soil receiving relatively high rainfall have abundant vegetation of relatively low quality to herbivores, because of the increase in structural tissue (lignin, fiber) needed for mechanical support by large plants (trees, bunchgrasses). The larger the individual herbivore, however, the wider its dietary tolerance and the greater its ability to utilize abundant low-quality forage that smaller herbivores cannot survive on. Body size and feeding style thus provide the basis for a first-order classification of functional types: small (<100 kg), medium (100–1,000 kg), large (>1,000 kg); grazers, mixed feeders, browsers (Bell, 1984). Finer categorizations have been proposed (Hempson et al., 2015) but a body size x feeding-style matrix (Figure 2) allows a visualization of how the composition of a large

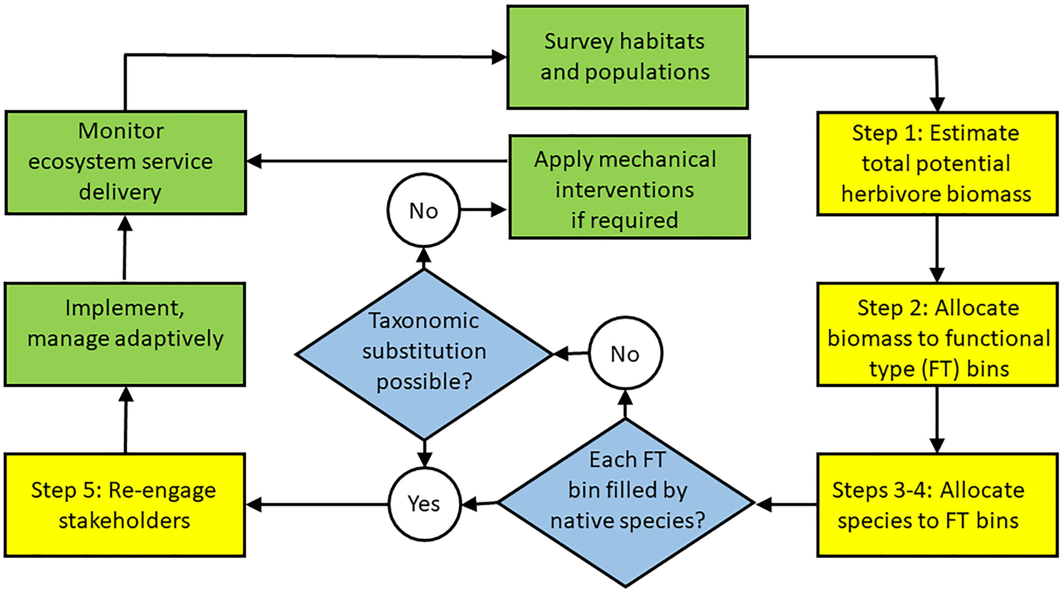

FIGURE 1
The process proposed to operationalize a rewilding project. Green boxes are actions performed by practitioners on the land. Yellow boxes are analyses performed in collaboration among practitioners, technical resources, and stakeholder groups, following steps described in the text. Blue diamonds are decisions on community assembly ultimately requiring ratification by stakeholders.

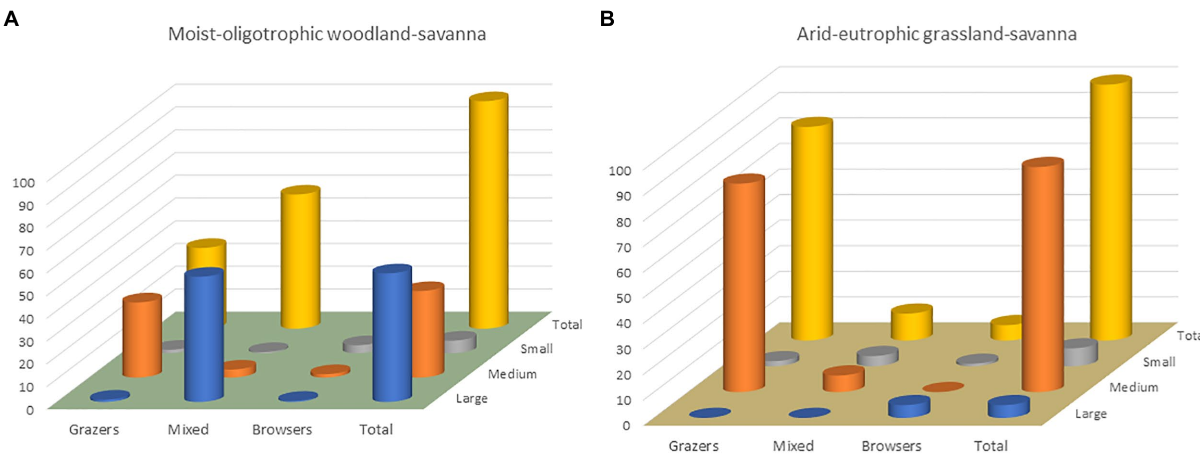

FIGURE 2
Distributions of large-herbivore community biomass (%) among functional types coarsely defined by feeding style (grazer, mixed feeder, browser) and body size (large, >1,000kg; medium, 100–1,000kg; small, <100kg) in two African savanna ecosystems: **(A)** a moist-oligotrophic woodland and **(B)** an arid-eutrophic grassland (data from Bell, 1984).

herbivore community can differ substantially between one ecosystem and another.

From historical wildlife survey data collected across African savannas, it is apparent that pure browsers (mainly giraffe, *Giraffa* spp. and black rhino, *Diceros bicornis*) generally contribute only ~10% or less to community biomass and across feeding styles the smallest body-size class (<10 kg) seldom represents >10% (Bell, 1984; Figure 2). Nevertheless, the most speciose size-class among African antelopes is 10–32 kg (du Toit and Cumming, 1999) and so the functional trait diversity of any one size class could be inversely related to its community biomass contribution. How generalizable these African patterns are at the global scale can be debated with the limited data on expected "natural" community structure for ecosystems on other continents. Paleoecological reconstructions for particular places at times prior to human disturbance are valuable for understanding species composition. Yet, for the total biomass of all syntopic species and the distribution of community biomass among functional types, the historical African data provide at least a guiding template formed by ecological principles (Bell, 1982) that are universal.

2.3. Prioritize ecosystem services and requisite functional traits

Rewilding projects aim to repair the functional properties of degraded ecosystems but the levels and types of degradation, and consequently the priorities for rewilding, differ between project areas. If a priority is the provision of herbaceous forage in an area encroached with woody vegetation, then requisite functional traits could be browsing, debarking, and seedling predation. If a priority is fire suppression then a requisite functional trait could be coarse grazing; if stream flow regulation then pond building; if revegetation then endozoochory; if soil amelioration then nutrient transport and tilling/rooting/churning; and so on. This step of prioritizing the functions needed from large herbivores sharpens the resolution of the body size x feeding style classification and sets up the next step of identifying species–with their requisite functional traits–to be prioritized by managers.

2.4. Prioritize native species but consider surrogates

After establishing a ballpark estimate of biomass density for the potential large herbivore assemblage in the area designated for rewilding, and then assigning a biomass distribution across the 3×3 matrix of body size classes and feeding styles (as in Figure 2), the rewilding planner now has nine "bins" of biomass to work with on paper. Native species can be allocated to each bin as appropriate, including species already in the project area and those that could be reintroduced. Then, species with required functional traits should be prioritized as above, ideally with redundancy because increased species richness in a large herbivore assemblage is associated with increased delivery of multiple ecosystem services (Maestre et al., 2022).

In most cases the megaherbivore (>1,000 kg) biomass bin is likely to remain empty due to extinctions, costs, and potential human-wildlife conflicts, but estimating the size of that bin is important for downsizing the overall biomass estimate. It might also be impossible or impractical to fill some other bins–while prioritizing required functional traits–with native species. In theory, non-native wildlife species could be considered as surrogates but in practice there are multiple legal, social, and economic barriers to that option. Nevertheless, various domestic species (horses, cattle, pigs, goats, sheep, etc.) can immediately be considered as surrogates and stocked together with native species at the densities required to fill those bins needing topping up.

Once all feasible biomass has been penciled in, and each species allocated a share of the biomass in its bin, the potential population of each species can be estimated simply by dividing its biomass by unit mass (⅔ adult female mass). Now, further adjustments can be made to account for population viability within the project area, with particular attention to social and economic viability. If a population is unlikely to be viable then it can be scratched and the population estimate for another species in that bin increased to take up the freed biomass.

2.5. Re-engage stakeholders

By this stage the project manager has an on-paper design of a large-herbivore assemblage that would be ecologically compatible with the area designated for rewilding, and would include the suite of functional traits required for the prioritized ecosystem services. Next, the stakeholders should be re-engaged for a decision-into-practice exercise (Butler et al., 2021). Using the on-paper design, the project manager can present a vision of the rewilding project with estimations on the likelihood of the project achieving its goals, at what costs (implementation, running, and opportunity costs), and over what timeframe. That presentation should include alternative scenarios for dealing with biomass bins that cannot be filled. For example, the missing megaherbivores could be functionally substituted to some extent by machinery (Bocherens, 2018), such as the mulching machines used for mastication of woodlands and shrublands in the western United States (Brennan and Keeley, 2017) where woody encroachment is a multi-billion-dollar problem (Morford et al., 2022). This would clearly infringe on the minimal-intervention ideals of rewilding but pragmatism might have to prevail for intermittent operations. Then, the implications of population regulation must be worked through for scenarios with and without an intact or partially intact predator community. Offtake through regulated hunting can control populations and earn revenue if stakeholders accept the ethical implications. Alternatively, populations can be allowed to self-regulate through density dependence, with die-offs in harsh years (Fløjgaard et al., 2022), requiring full recognition of the implications for animal welfare (Capozzelli et al., 2020).

Through a fully inclusive and equitable process, all stakeholders should be facilitated in their decision-making to reach consensus on whether to support or reject rewilding as a means toward meeting their needs and aspirations for the project area. If supported, then implementation should proceed with local participation in reintroduction operations, citizen-science surveys, field educational exercises, etc., to keep stakeholders engaged in *their* rewilding project.

3. Discussion

The stepwise, functionally-focused approach proposed here does not describe the ways in which most self-described rewilding projects (reviewed in Pettorelli et al., 2019) come into being. In Europe, the process most commonly involves one keystone species (Segar et al., 2022) after which the project progresses (or not) through learning-by-doing. That was a completely reasonable approach under past circumstances but now, with the rate of global change, the scale of the problem of faltering ecosystem services, and the growing interest in rewilding, there is a mounting need to equip the concept with a comprehensive plan for operationalization. Each case has its idiosyncrasies but the approach suggested here is aimed at the primary goal of establishing the range of ecological functions performed by a large herbivore assemblage in a terrestrial ecosystem. Thereafter, small carnivores will mostly take care of themselves whereas large carnivores, whether already present or not, require special considerations for rewilding (Linnell and Jackson, 2019).

Increasingly, conservation practitioners are having to abandon the ideal of restoring species composition to benchmark conditions and accept the existence of novel ecosystems (Hobbs et al., 2006). Such acceptance comes with the challenge of recognizing the value of the services that novel ecosystems can provide under present and forecast conditions. The rewilding concept holds promise for achieving the best–or perhaps least bad–alternative state that a self-organizing system could stabilize in and sustain the delivery of ecosystem services to its stakeholders. For land managers to visualize that state and articulate it to stakeholders requires tangible operational elements, and large herbivores are both compelling symbols of wildness and effective agents of key ecological processes. Furthermore, ecologically appropriate large-herbivore communities can be designed, assembled, and left to self-organize with minimal ongoing management. The ecological principles were revealed by foundational work in African savannas that took advantage of historical data on intact wildlife communities (Coe et al., 1976; Bell, 1982, 1984). Real-world application can be found in the extensive conversion of cattle ranches to private wildlife reserves and conservancies in southern and eastern Africa, where a rewilding movement of its own has been underway for decades now (Carruthers, 2008; Bothma and du Toit, 2016). There is no reason why the same ecological principles should not apply outside of African savannas where, in general, we can expect large-herbivore equilibrium biomass to vary predictably in response to primary productivity and soil nutrient availability. We can also expect the distribution of total biomass among functional types to differ predictably between ecosystem types.

In closing, a suggestion to facilitate the operationalization of the rewilding concept on a global scale is to develop typologies of functional types of animals and plants within bioregions of trait space (*sensu* Harris et al., 2022). These could be mapped in space and time by correspondence with latitude, climatic envelope, and soil nutrients. Each bioregion would have a generic (non-taxonomic) "parts list," which could be assembled (or allowed to self-assemble) in a project area from native species and surrogates as needed. The assembled community would optimally deliver ecosystem services and could be reorganized (or allowed to self-organize) as bioregions shift across the project area due to climate change. While this suggestion is likely heretical to conservation traditionalists, the dire and compounding ecological challenges of the Anthropocene demand non-traditional solutions.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

The author confirms being the sole contributor to this work and has approved it for publication.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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